

## Research article

# Diet and seed removal rates by the harvester ants *Pogonomyrmex rastratus* and *Pogonomyrmex pronotalis* in the central Monte desert, Argentina

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**Abstract.** Granivorous animals, through seed consumption, may have an important influence on plant abundance, distribution and species composition in desert ecosystems. The aims of this study are twofold: to quantify the diet of *Pogonomyrmex rastratus* (Mayr) and *Pogonomyrmex pronotalis* (Santschi), and to estimate seed removal per colony of both species throughout their activity season (October–April) in the central Monte desert, Argentina. Both species rely heavily upon seeds, which account for 87–94% of the items carried to the nests. Their diets are similar, consisting mainly of grass seeds, which represent more than 93% of the seeds. Among them, three species predominate: *Aristida* spp., *Trichloris crinita* and *Pappophorum* spp. Seasonal variations as well as seed species richness in the diet are also similar between species. However, their food-handling behaviour differs: most caryopses carried by *P. pronotalis* bear bracts whereas most caryopses carried by *P. rastratus* lack them. Seed removal per colony by *P. rastratus* ( $6 \times 10^4$  seeds/colony) and by *P. pronotalis* ( $5 \times 10^4$  seeds/colony) throughout the season is similar to the one reported for *P. occidentalis* in North America. However, seed removal per hectare, which could be estimated for *P. rastratus* ( $8.3 \times 10^5$  seeds/ha), is lower than removal rates reported for the North American species *P. barbatus*, *P. desertorum*, *P. rugosus* and *P. californicus*, probably because *P. rastratus* has lower activity levels and smaller colonies than the North American studied species.

**Keywords:** Harvester ants, granivory, foraging activity, *Pogonomyrmex pronotalis*, *Pogonomyrmex rastratus*.

## Introduction

Seeds constitute the only means of dispersal and access to new regions for most desert plants (Kemp, 1989). Thus

seed consumption by granivorous animals, such as small mammals, birds and ants, may have an important influence on desert plant communities (Brown et al., 1979; Inouye et al., 1980; Louda, 1989; Heske et al., 1993; Guo et al., 1995; Mull and MacMahon, 1996).

Harvester ants are especially common in arid and semi-arid areas. Among them, the genus *Pogonomyrmex* comprises about 60 species in North, Central and South America (Hölldobler and Wilson, 1990; Taber, 1998; MacMahon et al., 2000). Some North American species, which have been extensively studied, make up the bulk of desert ant assemblages and play an important role in desert ecology (MacMahon et al., 2000). Most species studied are strict granivores (Whitford, 1978; Mehlhop and Scott, 1983; Hölldobler and Wilson, 1990; MacKay, 1991; Taber, 1998; Johnson, 2000) and capable of removing a large number of seeds (Tschinkel, 1999). However, most estimates of the fraction of total seed production removed by harvester ants have been less than 10% (Pulliam and Brand, 1975; Whitford, 1978; Crist and MacMahon, 1992). This impact turns out to be much greater on preferred species (Pulliam and Brand, 1975; Whitford, 1978) even attaining a complete removal of seeds available (Crist and MacMahon, 1992). This selective removal can alter the relative abundance of plant species causing changes in the structure of plant communities (Brown et al., 1979; Inouye et al., 1980).

In the central Monte desert (Argentina), ants are the most important granivores in spring and summer (Lopez de Casenave et al., 1998; Marone et al., 2000). There are about 26 species capable of removing seeds, including species of the genera *Pogonomyrmex*, *Pheidole* and *Solenopsis* (Marone et al., 2000; J. Lopez de Casenave et al., unpubl.). However, no studies have been performed on the composition of the diet of these species to see the extent to which they rely on seeds. Moreover, their seed removal hasn't been quantified, so little is known about their actual importance

as granivores. *Pogonomyrmex rastratus* (Mayr) and *P. pronotalis* (Santschi) occur in the central Monte desert (Claver and Fowler, 1993). There, their activity season spans from October to April and they present a diurnal activity throughout the season with temporal changes responding mainly to soil temperatures (Pol and Lopez de Casenave, 2004). They seem to display smaller colonies and to have lower population densities than their studied counterparts in North America but they appear to be highly specialised granivores (Kusnezov, 1951; Marone et al., 2000). The aims of this study are (1) to quantify the diet of *P. rastratus* and *P. pronotalis* and (2) to estimate seed removal per colony of both species throughout their activity season (October–April) in the central Monte desert.

## Methods

### Study site

The study was carried out in the open woodland at the Biosphere Reserve of Nacuñán (34°03'S–67°54'W), located in the central portion of the Monte desert, Mendoza Province, Argentina. The main habitat of the reserve is the open woodland of *Prosopis flexuosa* where individuals of this species and of *Geoffroea decorticans* are scattered within a matrix of perennial tall shrubs (>1 m height, mostly creosotebush *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa* and *Larrea cuneifolia*), low shrubs (*Lycium* spp., *Junellia aspera* and *Acantholippia seriphioides*), and perennial grasses (e.g., *Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida* spp., *Digitaria californica*, *Setaria leucopila*). Annual forb cover (e.g., *Chenopodium papulosum*, *Phacelia artemisioides*, *Parthenium hysterophorus*) is highly variable from year to year.

Nacuñán's climate is dry and temperate with cold winters. Mean annual precipitation is 338 mm (1972–2000), very variable between years. Seventy five percent of the annual rainfall occurs in spring and summer (October–March), and seed production of almost all plants is restricted to summer months.

### Diet sampling

The diet of *Pogonomyrmex rastratus* and *P. pronotalis* was evaluated using two simultaneous techniques: (1) direct collection of items from returning foragers and (2) collection with a semi-automated device. For (1), at least 20 foragers with their loads were collected with forceps and a teaspoon at each colony on every sampling occasion. Technique (2) consisted in the collection of returning foragers with a semi-automated device, based on Crist and MacMahon's (1991). Our version of it was a circular plastic enclosure (33 cm diameter, 10 cm tall) placed around the nest entrance, low enough to allow air circulation and transparent so it never shaded the nest. Each enclosure had four pairs of openings 90° apart and 3 cm above the ground, consisting of one "entrance" and one "exit" each. Soil ramps allowed ants to access these ports on the corresponding side of the enclosure. As these ants are bad climbers (like other species of the same genus; Gordon, 1999), they were unable to climb the 3 cm vertical rise on the opposite side of the "entrance" or "exit" and thus they were prevented from using the exit port as an entrance or vice versa. Pitfall traps (plastic containers 3 cm diameter, 5 cm deep) with removable covers were set into the ground inside the enclosure, flush with the entrance but 3 cm above the ground. The device was placed the day prior to the sampling to minimise disturbance on the sampling day and to allow ants to learn the appropriate paths in and out the enclosure. On each of two sampling days, trap covers were removed during the periods of high activity in the morning and the af-

ternoon (according to Pol and Lopez de Casenave, 2004) totalling two hours of sampling per colony a day. Incoming ants captured during the sampling were counted and released near the nest entrance. Their forage was collected for further analysis. Covers were placed again on the traps after each sampling period allowing normal forage activity during non-sampling periods.

These species begin to forage by October and cease their foraging activity throughout the autumn (Pol and Lopez de Casenave, 2004). The study was carried out spanning 2000–2001 activity season on four occasions (October and December 2000, February and April 2001). The original design envisioned the sampling of the same five randomly chosen colonies of *P. pronotalis* and *P. rastratus* through time. However, due to the low activity levels found in October (Pol and Lopez de Casenave, 2004), the expected number of colonies could not be sampled. Moreover, many of the originally chosen colonies decreased or ceased their activity during the season (which is not unusual in this genus, Taber, 1998; see also Pol and Lopez de Casenave, 2004). This made us choose others to keep the number of replicates, and therefore to work with different colonies throughout the study period.

The items collected from foragers were counted and identified in the laboratory. We considered one item as the load carried by one forager. This definition of item underestimates the importance of those items made up of more than one unity (e.g., one spikelet of *Pappophorum* spp. can contain up to four caryopses). Each item was assigned to a category: seeds, flowers, fruits (all fruits excluding grass caryopses which were included in seeds; see Whitford, 1978), vegetative plant parts (non-reproductive structures of plants such as whole leaves or parts of them, and twigs), invertebrates (entire organisms as well as parts of them) and other items. Seeds were identified to genus (e.g., *Pappophorum* spp., *Aristida* spp.) or species level and for grass caryopses the presence or absence of vegetative bracts (glumes, palea and lemma) was recorded.

### Data analysis

*P. rastratus*' and *P. pronotalis*' diet was evaluated by averaging the percentage which represents each type of item or seed species among colonies (i.e., the experimental units) on each sampling occasion. Percentages of each type of item were averaged across sampling occasions to estimate the diet composition during one season. Seed species richness in the diet was calculated likewise but averaging the number of seed species per colony. Data obtained from both sampling techniques were analysed together. This allows a more complete assessment of the diet and also increases the number of items per nest, improving the estimation. The Spearman rank-order correlations for results of percentages of seed species in the diet from both techniques were significant ( $r = 0.67, 0.76, 0.64$  and  $0.85$  for *P. pronotalis*, and  $r = 0.63, 0.59, 0.84$  and  $0.56$  for *P. rastratus* in October, December, February and April, respectively;  $p < 0.05$  in all cases). Two-tailed Mann-Whitney tests were performed to compare the percentage of each seed species in the diet of *P. pronotalis* and *P. rastratus* on every sample occasion, except for October, when the number of colonies sampled was too low. Among-month differences in each ant species' diet could not be statistically assessed because we did not sample the same five colonies throughout the study period (which would have allowed us to use a repeated measures design) but several colonies were included on more than a single occasion (thus violating the independence assumption for a standard test). For this reason, we only show trends in the data.

In order to assess if *P. pronotalis* and *P. rastratus* carried similar proportions of caryopses with and without bracts, Chi-square tests were performed for the most abundant species in the diet (*Aristida* spp., *Pappophorum* spp., *Trichloris crinita*, *Stipa ichu*, *Chloris castilloana* and *Digitaria californica*). For this analysis, we pooled data from different colonies and different sampling occasions, and used each seed carried to the nest as a datum. In doing so, we are considering the handling behaviour of an individual ant (i.e., their decision of removing the bracts from a certain caryopsis) independent of that of the other individuals from the same colony.

	Seeds	Vegetative plant parts	Flowers	Invertebrates	Fruits	Other items	Total number of items
<i>Pogonomyrmex pronotalis</i>	87.3 ± 3.9	4.2 ± 0.8	4.4 ± 4.1	1.4 ± 0.6	0.7 ± 0.2	2.1 ± 0.3	1451
<i>Pogonomyrmex rastratus</i>	93.8 ± 2.3	2.7 ± 0.6	0.8 ± 0.7	0.6 ± 0.6	0.1 ± 0.1	2.0 ± 1.2	932

**Table 1.** Mean (± SE) percentage of different food items in the diet of *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the central Monte desert across the 2000–2001 activity season. Number of colonies sampled: two in October and five in December, February and April for both species.

**Table 2.** Mean (± SE) percentage of seeds of different plant species in the diet of *Pogonomyrmex pronotalis* (PP) and *Pogonomyrmex rastratus* (PR) in the central Monte desert during 2000–2001 activity season. Forb species recorded were *Chenopodium papulosum*, *Conyza* spp., *Parthenium hysterophorus*, *Descurainia* spp. and *Lappula redowski*. Shrub species were *Lycium* spp., *Junellia aspera*, *Larrea* spp. and *Acantholippia seriphoides*. Number of seed species recorded and total number of seeds collected are given. Number of colonies sampled are the same as in Table 1.

	October		December		February		April	
	PP	PR	PP	PR	PP	PR	PP	PR
Grasses	93.4 ± 0.3	97.9 ± 2.1	97.6 ± 1.4	98.8 ± 0.7	97.1 ± 1.6	98.2 ± 0.7	96.5 ± 1.6	100
<i>Aristida</i> spp.	90.1 ± 0.5	95.8 ± 4.2	44.7 ± 13.4	36.5 ± 8.0	68.9 ± 9.6	53.8 ± 12.1	88.9 ± 5.0	87.4 ± 6.1
<i>Trichloris crinita</i>	1.6 ± 1.6	–	27.9 ± 8.7	15.2 ± 5.2	20.4 ± 13.4	32.5 ± 10.1	4.0 ± 2.4	6.2 ± 5.6
<i>Pappophorum</i> spp.	1.7 ± 1.7	2.1 ± 2.1	17.2 ± 6.4	22.0 ± 6.9	2.1 ± 4.5	10.2 ± 4.8	–	0.9 ± 0.9
<i>Digitaria californica</i>	–	–	1.2 ± 0.5	0.7 ± 0.7	2.8 ± 1.1	0.2 ± 0.2	0.4 ± 0.4	–
<i>Chloris castilloana</i>	–	–	0.4 ± 0.4	0.4 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	2.8 ± 1.5	5.5 ± 4.9
<i>Setaria leucopila</i>	–	–	2.0 ± 1.9	–	1.7 ± 1.5	–	–	–
<i>Sporobolus cryptandrus</i>	–	–	0.7 ± 0.7	5.1 ± 5.1	0.3 ± 0.2	–	–	–
<i>Stipa ichu</i>	–	–	3.1 ± 2.0	19.0 ± 8.1	0.6 ± 0.3	1.5 ± 0.9	0.4 ± 0.4	–
<i>Diplachne dubia</i>	–	–	0.3 ± 0.3	–	0.3 ± 0.3	–	–	–
Forbs	1.6 ± 1.6	2.1 ± 2.1	1.1 ± 0.6	1.1 ± 0.7	1.9 ± 1.1	1.6 ± 0.8	–	–
Shrubs	5.0 ± 1.2	–	1.0 ± 0.6	0.2 ± 0.2	1.0 ± 0.6	0.1 ± 0.1	3.5 ± 1.6	–
Number of species	3.5 ± 0.5	2.0 ± 1.0	5.8 ± 1.0	5.2 ± 0.4	7.0 ± 1.9	4.6 ± 0.5	3.6 ± 1.0	2.0 ± 0.6
Number of seeds	61	28	347	394	710	379	203	98

*Seed removal rates*

Number of seeds foraged per colony was assessed on the basis of foraging activity levels. Pol and Lopez de Casenave (2004) estimated the number of workers that returned to the nest (with or without forage) every hour (*WH*) during a day. The sum of these values for each occasion multiplied by the number of days per month (*DM*) estimates the number of foragers that enter the nest in one month. As not all foragers return to the nest with a load, the data were multiplied by a forager success correction factor (*FS*: proportion of workers which return to the nest with a seed) which was estimated for each species on every sampling occasion with data from the semi-automated device (as number of seeds found in traps/number of ants captured). The following formula synthesises the calculus of seed removal per colony per month (*RC*):

$$RC_i = DM_i \times FS_i \times \sum_{j=1}^{24} WH_{ij};$$

where *i* stands for sampling month and *j* for the time of the day.

To estimate ants' seed removal during the whole season (October–April), November's removal values were extrapolated from October's, January's from December's and March's from February's. Removal of *Aristida* spp., *Trichloris crinita* and *Pappophorum* spp. was calculated by

multiplying removal per colony by the proportion of each of these species in the diet in the corresponding period. The levels of activity correspond to ideal hot and cloudless days (Pol and Lopez de Casenave, 2004).

**Results**

Throughout the activity season *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* carried seeds, flowers, fruits, vegetative plant parts (e.g., remains of leaves and twigs), invertebrates (in most cases parts of dead arthropods) and other items (e.g., vertebrate feces, mosses, lichens) to their nests. These species rely heavily upon seeds, which accounted for 87 and 94 % of the food items carried to the nests by *P. pronotalis* and *P. rastratus*, respectively (Table 1). Among the other categories vegetative plant parts was the most abundant one, but all of them were poorly represented. The only exception was a relatively high proportion of flowers carried by *P. pronotalis* in October (17 %) which was the result of

**Table 3.** Percentage of grass caryopses lacking bracts (glumes, palea and lemma) carried to the nest by *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the central Monte desert across the 2000–2001 activity season. The total number of seeds examined is shown between brackets. Results of Chi-square tests comparing the frequency of caryopses lacking bracts carried by *P. pronotalis* and *P. rastratus* are also shown.

Seed species	<i>P. pronotalis</i>	<i>P. rastratus</i>	P
<i>Aristida</i> spp.	0.1 (1053)	29.0 (503)	<0.0001
<i>Trichloris crinita</i>	3.7 (437)	96.1 (259)	<0.0001
<i>Pappophorum</i> spp.	1.7 (230)	96.7 (242)	<0.0001
<i>Chloris castilloana</i>	5.0 (40)	62.5 (16)	<0.0001
<i>Stipa ichu</i>	0 (23)	28.2 (39)	0.0137
<i>Digitaria californica</i>	2.3 (89)	23.9 (46)	0.000

the exceptionally high proportion of *Atriplex lampa*'s flowers carried by one of the two colonies sampled.

Grass seeds predominated in both species' diet (more than 93% of the seeds in all sampling occasions) whereas forb and shrub seeds were always scarce (Table 2). Three grass species (*Aristida* spp., *Trichloris crinita* and *Pappophorum* spp.) accounted for more than 90% of the seeds carried by both species on all sampling occasions. Only in December a fourth species, *Stipa ichu*, reached a relatively high proportion in the diet of *P. rastratus*. *Aristida* spp. was the most carried species during the whole season but its proportion decreased in December and February when the proportions of *Trichloris crinita* and *Pappophorum* spp. increased (Table 2). No significant differences between *P. pronotalis*' and *P. rastratus*' diet were found when the percentages of each seed species and species richness were compared for each sampling occasion (Mann-Whitney test,  $p > 0.05$ ).

*P. rastratus* carried a significantly higher proportion of grass caryopses without bracts than *P. pronotalis* did (Table 3). Almost all *Trichloris crinita*'s and *Pappophorum* spp.'s caryopses, 63% of *Chloris castilloana*'s, 29% of *Aristida* spp.'s, 28% of *Stipa ichu*'s and 24% of *Digitaria californica*'s caryopses carried by *P. rastratus* lacked bracts. Additionally, most caryopses that bore bracts lacked glumes. Conversely, *P. pronotalis* carried caryopses with glumes, palea and lemma almost invariably.

The total number of seeds removed per colony by the end of the season was higher for *P. rastratus* than for *P. pronotalis* ( $6.0 \times 10^4$  and  $4.9 \times 10^4$  seeds per colony, respectively). Both species removed similar quantities of *Aristida* spp. and *Trichloris crinita* seeds (*P. pronotalis*,  $3.1 \times 10^4$  and  $1.0 \times 10^4$ ; *P. rastratus*  $2.9 \times 10^4$  and  $1.2 \times 10^4$  seeds of *Aristida* spp. and *Trichloris crinita*, respectively), but *P. rastratus* removed almost three times as much *Pappophorum* spp. as *P. pronotalis* did ( $9.8 \times 10^3$  vs.  $3.5 \times 10^3$ ). *P. pronotalis* removed the highest number of seeds in February–March whereas *P. rastratus* did it in December–January. These temporal variations are partly the result of differences in the activity levels along the season (Pol and Lopez de Casenave, 2004). Foraging success also varied among sampling occasions (the

proportion of *P. pronotalis*' and *P. rastratus*' workers which returned to the nest with a seed, varied between 0.43–0.67 and 0.51–0.86, respectively).

## Discussion

*Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* rely heavily upon seeds as most *Pogonomyrmex* do (Whitford, 1978; Mehlhop and Scott, 1983; Hölldobler and Wilson, 1990; MacKay, 1991; Taber, 1998). Nonseed items returned to the nest (flowers, fruits, leaves, twigs, dead arthropods and vertebrate feces) have been observed in other *Pogonomyrmex* species, also in low proportions (Whitford, 1978; Chew and De Vita, 1980; Davidson, 1980; Mehlhop and Scott, 1983; Hölldobler, 1986; Hölldobler and Wilson, 1990; MacKay, 1991). However, the proportion of *Atriplex lampa*'s flowers was high in *P. pronotalis*' diet in October. Although this was the result of the high consumption of only one of the two colonies studied, this behaviour of *P. pronotalis* seems to be common at the beginning of the season, when the abundance of mature seeds is low and *Atriplex lampa*'s flowers abound (S. Claver et al., unpubl.; J. Lopez de Casenave, pers. obs.). Live prey, especially termites, which may occur in the diet of some *Pogonomyrmex*, namely *P. californicus*, *P. rugosus* and *P. desertorum* (Whitford, 1978), *P. maricopa*, *P. apache* and *P. barbatus* (Taber, 1998), were absent from *P. pronotalis*' and *P. rastratus*' diet during the studied period.

Grass seeds predominate among all seeds included in the diet of *P. pronotalis* and *P. rastratus*. Only three species, *Aristida* spp., *Pappophorum* spp. and *Trichloris crinita*, account for the great bulk of the seeds harvested by these ants. In North America, where the diet of some *Pogonomyrmex* species has been well studied, grass seeds also prevailed (Pulliam and Brand, 1975; Whitford, 1978; Crist and MacMahon, 1992; Taber, 1998; Gordon, 1999; MacMahon et al., 2000).

Grass seeds may be prevalent in these species' diet because they seem to be a more predictable resource than ephemeral forb seeds in the central Monte desert. Most grasses are perennial and produce seeds even during dry years (Kemp, 1989; R. Pol et al., unpubl.) whereas forb seed production depends highly on precipitation, which is extremely variable interannually. Seed abundance could also be important in determining seed selection (MacMahon et al., 2000) but in the central Monte desert forb seeds are more abundant than grass seeds in the soil seed bank (Marone et al., 1998). Grass seeds also have a low concentration of secondary compounds (Díaz, 1996) which may act as repellents for ants (Buckley, 1982). Seed size has also been suggested as an important attribute that could influence seed selection (Mehlhop and Scott, 1983; Crist and MacMahon, 1992; Morehead and Feener, 1998; Detrain and Pasteels, 2000; Willott et al., 2000). In our study, ants carried seeds ranging from 0.04 to 2.93 mg (see Marone et al., 1998), but even though size range of forbs in the diet was similar to grasses' (0.04 to 0.45 vs. 0.06 to 0.60 mg), they were less consumed. Thus, seed size alone doesn't seem explain the prevalence

of grass seeds in these ants' diet. Seed morphology can also influence ants' choices (Pulliam and Brand, 1975). These authors noticed that most seeds carried by *P. barbatus* were elongated and bore conspicuous awns, hairs and other projections providing the ants with a rough surface to grasp, while rounded seeds with smooth outlines were only taken when they were still attached to a seed head. In our study, the presence of awns, hairs or projections may not be relevant as *P. rastratus* carried a high proportion of seeds without bracts but its diet was similar to that of *P. pronotalis*. The shape of the seed, nevertheless, could affect seed selection because the three most abundant species in their diet, *Aristida* spp., *Trichloris crinita* and *Pappohorum* spp., are elongated whereas the rounded seeds of *Setaria leucopila* and *Sporobolus cryptandrus* were rarely harvested even though they are the heaviest and the most abundant grasses in the soil seed bank, respectively (Marone et al., 1998). But, again, the rough and variably shaped seeds of forbs were seldom taken. Nutritional quality (Kelrick et al., 1986, Crist and MacMahon, 1992) could influence seed selection, although we have no data on differences in this characteristic between grass and forb seeds which could explain the prevalence of grasses in the diet. We suggest that there may be a hierarchy among attributes which determine seed selection. Predictability and absence of secondary compounds could determine the selection of grass over forb seeds, and at a lower level, other attributes such as morphology could determine the selection among grasses. More detailed studies as regards mechanisms of seed preferences which take into account chemical, nutritional and morphometrical traits of the seeds remain to be performed.

Several authors have predicted that sympatric granivorous ants should show shifts in resource utilisation in time and space or differences in foraging strategies as a result of competitive interactions which structure ant communities (Davidson, 1977; Whitford, 1978; Brown et al., 1979; Mehlhop and Scott, 1983; Hölldobler and Wilson, 1990). In the central Monte desert, where *P. pronotalis* and *P. rastratus* coexist, their diets overlap in composition, species richness and seasonal variations. Moreover, their daily and seasonal foraging periods coincide (Pol and Lopez de Casenave, 2004), they show the same foraging strategy (R. Pol and J. Lopez de Casenave, unpubl.) and their nests are not spatially segregated (J. Lopez de Casenave and F. Milesi, unpubl.). Thus, should any difference exist, it was not detected in the variables measured so far.

*P. rastratus* and *P. pronotalis* differ in their food-handling behaviour. The former carries a greater proportion of seeds lacking bracts than the latter do. Moreover, observations of individual foraging behaviour of *P. rastratus*' workers in the field show that this species spends longer manipulating seeds during foraging trips, principally due to the partial or complete removal of bracts before carrying them to the nest (R. Pol and J. Lopez de Casenave, unpubl.). This behaviour explains the absence of chaff piles around this species' nests. In contrast, around *P. pronotalis*' nests there is some accumulation of such material, particularly during high activity months, showing that removal of nonedible parts of seeds

takes place inside the nest. Food-handling differences have been observed among various species of the genus *Pogonomyrmex* (Taber, 1998). For instance, *P. badius*, *P. barbatus* and *P. occidentalis* remove the nonedible parts of the seeds before storing them inside the granaries whereas other species, such as *P. coarctatus*, don't remove them until the seeds are consumed (Taber, 1998).

The estimated number of seeds removed per colony by *P. pronotalis* and *P. rastratus* during the study season (ca. 50,000 and 60,000, respectively) in the central Monte desert was similar to the one reported by Crist and MacMahon (1992) for *P. occidentalis* (53,100 and 81,300 in two consecutive seasons) in a shrub-steppe ecosystem in Wyoming. Seed removal per hectare could be assessed by multiplying seed removal per colony by colony density per hectare. We estimated colony density by counting the colonies in two 50 × 50 m plots on each sampling occasion during high activity periods in the morning and in the afternoon (see Pirk et al., 2004). We could not estimate seed removal per hectare for *P. pronotalis* as none of its colonies was detected under this sampling intensity. This does not mean that *P. pronotalis* is absent from the open woodland (in fact, colonies for the diet sampling in this study were located there) but that its colony densities are probably very low in this habitat. We have observed that colonies occur more frequently in and near the roads which cross the reserve (Pirk et al., 2004). By the end of the season *P. rastratus* had removed about  $8.3 \times 10^5$  seeds/ha, which is much lower than the values reported for *P. barbatus* ( $6.5 \times 10^6$  seeds/ha; Pulliam and Brand, 1975) or for *P. desertorum*, *P. rugosus* and *P. californicus* ( $1.9 \times 10^7$  seeds/ha for the three species only during August; Whitford, 1978). *P. rastratus*' low estimated seed removal rates are associated to lower colony densities (a maximum of 16 active colonies/ha in February) than in other species studied in North America, such as *P. rugosus*, *P. desertorum* and *P. californicus* (21, 138 and 45 colonies/ha, respectively, in the Chihuahuan desert; Whitford and Ettershank, 1975), and *P. occidentalis* (around 30 colonies/ha in Wyoming; Parmenter and MacMahon, 1983). Furthermore, activity levels also seem to be lower (Pol and Lopez de Casenave, 2004): they represented less than 25% of the rates reported for *P. occidentalis* (Crist and MacMahon, 1991). The values of foraging success, which range from 43% to 86%, don't differ much from the reported ones for other *Pogonomyrmex* (Davidson, 1977; Whitford, 1978; Gordon, 1999). Nevertheless, it has to be taken into account that we are comparing these species with the most studied species in North America which have generally large and high density colonies (Johnson, 2000). In order to put our results in perspective we should also consider congeners with small and less obvious colonies (e.g., *P. anzensis*, *P. bicolor*, *P. bigbendensis*, *P. huachucae*, *P. tenuispina* and *P. texanus*; Taber, 1998) which haven't been so thoroughly studied.

Although in most studies where seed removal by ants was compared with seed production the fraction removed by harvester ants has been 10% or less, ants can have a greater impact on the seeds of preferred species (MacMahon et al., 2000). For example, *Messor pergandei* harvests less than

1% of the available seeds in the Mojave desert but could have a significant effect on preferred species (Tevis, 1958), *Pogonomyrmex* spp. remove a significant fraction of the seed production of *Bouteloua barbata* in the Chihuahuan desert (Whitford, 1978), whereas *P. occidentalis* remove 9–26% of the seed pool but as much as 100% of the *Alyssum desertorum* seeds in Wyoming (Crist and MacMahon, 1992). We have no estimates of seed production in the central Monte desert for our study period. However, and only in terms of making a rough comparison and with no consideration of the consumption of some recently produced seeds or the interannual variability, we used data on the seeds on the soil seed bank in February 1995 reported by Marone et al. (1998). According to these data, *P. rastratus* would be removing about 1% of the total seeds in the soil seed bank, 7% of *Trichloris crinita*'s, 15% of *Pappophorum* spp.' and the total of *Aristida* spp.' seeds. It has to be noted that these values could be rather conservative as the other *Pogonomyrmex* species inhabiting Ñacuñán (*P. pronotalis* and *P. inermis*), as well as other ants with a potential impact (Marone et al., 2000; J. Lopez de Casenave et al., unpubl.), were not included. These figures suggest that this selective ant could have a significant effect on seed reserves of one of the species consumed (*Aristida* spp.), as reported for other harvester ants. Of course, detailed studies addressing this particular issue are needed to draw any firm conclusion on the potential impact of these ants on the soil seed banks.

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